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RESEARCH ARTICLE

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Ecosystem services and disservices by birds, bats and monkeys change with macadamia landscape heterogeneity

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Abstract

1. The relative importance of ecosystem services and disservices can change with landscape structure in a poorly understood way.
2. We compare the impact of biocontrol, provided by bats and birds, with that of crop raiding by vervet monkeys on yield in South African macadamia orchards. Insectivorous bats and birds are known to feed on macadamia pest insect species, like the macadamia nut borer or the green vegetable bug. Vervet monkeys move into the orchards during the day to feed on premature macadamia nuts. Bats, birds and monkeys benefit from patches of natural vegetation adjacent to orchards.
3. With exclusion experiments (four treatments: day, night, day and night, control) we quantified the relative importance of biocontrol and crop raiding on yield, comparing two different landscape settings of the orchards, a natural and a human-modified.
4. Crop raiding occurred only close to natural vegetation and caused yield losses of about 26%. Biocontrol by bats and birds was higher near natural vegetation, but still significant in human-modified landscapes, at up to 530 m distance to forest patches. Prevented biocontrol through the exclusion of bats and birds resulted in yield losses of up to 60%.
5. Effects of biocontrol by bats and birds (USD ~5,000 ha/year) were economically more important than the losses of crop raiding (USD ~1,600 ha/year). As both are linked to the vicinity of forest patches, the removal of natural vegetation to limit monkey abundances would also limit biocontrol service provision.
6. *Synthesis and applications*. This study highlights the high economic benefits of biocontrol by bats and birds, which outweighed negative impacts through yield losses caused by crop raiding monkeys. Management practices to prevent crop damage, such as guarding, excluding vertebrates or removal of adjacent natural vegetation, would also limit access for bats and birds and the great economic benefits provided by their biocontrol. Ecosystem services by bats and birds can be promoted by the exposure of artificial roost and nest sites, but research into species-specific preferences is needed. The education of farmers is crucial, as many are unaware

of the benefits from birds and bats and the fact that these benefits can outweigh the disadvantages of the monkeys' crop raiding.

KEYWORDS
agricultural landscape, biocontrol, crop raiding, exclusion experiments, natural landscape, pest control, trade-off, vervet monkey

1 | INTRODUCTION

Nature provides well known ecosystem services (ES) as well as disservices (EDS). The interaction of the two is however less understood. To make optimal use of ES and minimize the negative effects of EDS, further research into management strategies to enhance ES and to limit or even prevent EDS are necessary (Vaz et al., 2017). In agriculture both can have important economic impacts. Bennett, Peterson, and Gordon (2009) call for a better understanding of the relationship of different ES, not considering the potential role of EDS, while Saunders, Peisley, Rader, and Luck (2016) recognize the interaction of both and the need for combined research. EDS are defined as either reducing productivity or increasing production costs (Zhang, Ricketts, Kremen, Carney, & Swinton, 2007). Primates are widely known crop raiders and often cause EDS, as established in several qualitative surveys (Weyell et al., 2015; Naughton-Treves, Treves, Chapman, & Wrangham, 1998; Saj, Sicotte, & Paterson, 2001; Sigwela, Elbakidze, Powell, & Angelstam, 2017; Tweheyo, Hill, & Obua, 2005), while quantitative research is scarce (Weyell et al., 2015; Wallace & Hill, 2012; Zhang et al., 2007). In Africa and Asia, where primates are believed to account for the majority of crop damages (Naughton-Treves et al., 1998), their impact can be especially high. It is believed that almost all primate species engage in crop raiding, but old world monkeys (Cercopithecidae) are particularly known crop raiders, due to their opportunistic foraging behaviour (Lee & Priston, 2005). Damage by primates is related to vicinity to forests and decreases with increasing distance to forest edges (Ango, Börjeson, & Senbeta, 2017; Lemessa, Hylander, & Hambäck, 2013; Saj et al., 2001; Wallace & Hill, 2012).

Flying vertebrates, such as bats and birds, are well known ES providers (Kunz, Braun de Torrez, Bauer, Lobova, & Fleming, 2011; Sekercioglu, 2006) and act, amongst others, as pest control agents (Boyles, Cryan, McCracken, & Kunz, 2011; Jones, Purvis, & Gittleman, 2003; Mols & Visser, 2007; Williams-Guillen, Perfecto, & Vandermeer, 2008). The economic impact of bats and birds on biological insect-pest control has been the focus of scientific research. Based on a recent global review, estimates of the economic value of bat predation in different agro-ecosystems ranged from 0 to 757$ / ha/year or up to 47% of the value of annual production (Taylor, Grass, Alberts, Joubert, & Tscharntke, 2018). These effects are mediated through trophic cascades in arthropod communities initiated by predation by both bats and birds (Maas, Karp, et al., 2015). Both ES and EDS change with landscape structure (Kremen, 2005; Kremen et al., 2007; Rusch et al., 2016; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005) and farmers often view remaining natural areas as lost area or even a cost, where natural habitats promote pests (Tscharntke et al., 2016). The loss of natural habitats and their fragmentation may result in the loss of service providers as well as higher crop raiding rates. There may hence be a trade-off between ES and EDS mediated by landscape composition.

In this study, we look into the trade-off between the ES of biological control by flying vertebrates and the EDS of crop raiding monkeys in macadamia nut orchards in South Africa. One major threat to the macadamia production in South Africa is kernel damage by pest insects (Schoeman & de Villiers, 2015). In 2017, Heteroptera caused an economic loss to the South African macadamia industry of USD 6,823,827 (Southern African Macadamia Growers' Association, unpublished data). Farmers also experience high crop raiding pressure from the Vervet monkey *Chlorocebus pygerythrus*, inhabiting patches of natural vegetation in and around agricultural land. A recent survey by the South African Macadamia Growers Association suggests that monkeys and baboons cause an annual loss of USD 5,251,648 to South African growers (Southern African Macadamia Growers' Association, unpublished data).

We aimed to quantify not only the economic impact of insect-pest controlling services of flying vertebrates, but also the trade-off between their positive impact and the negative effects of crop raiding vervet monkeys close to natural vegetation, by means of a 3 year long vertebrate exclusion experiment in two different landscape settings (natural and human-modified).

We hypothesized (Figure 1a) that (1) the absence of bats and birds increases insect damage to the macadamias, thereby decreasing nut quality, (2) macadamia yield decreases due to early abortion of damaged nuts where bats and birds are excluded, and (3) the effect of bat and bird exclusion is stronger next to natural vegetation. With respect to crop raiding by monkeys we hypothesized (1) that macadamia yield increases significantly where monkeys have been excluded, but (2) that this is only true for the exclusions adjacent to natural landscapes (where monkeys are present).

2 | MATERIALS AND METHODS

2.1 | Study area, study organisms and the agro-ecosystem

Macadamias *Macadamia integrifolia* have been cultivated in Levubu, Limpopo, for more than 60 years. The macadamia is a tree nut native to Australia (Nagao, Hirae, & Stephenson, 1992). Trees are mass

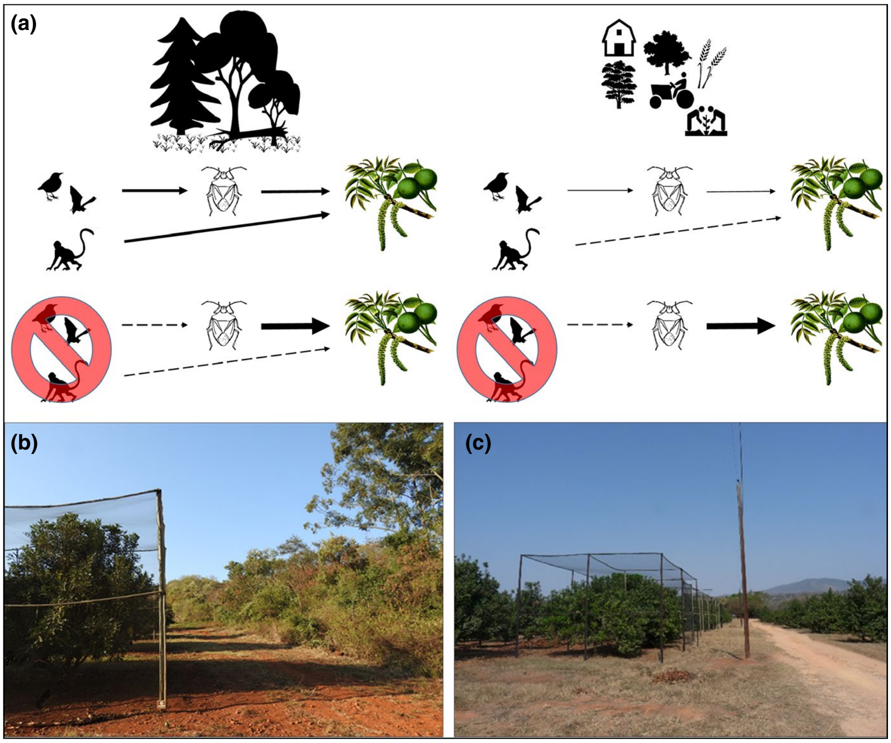


FIGURE 1 (a) Graphical presentation of the main hypotheses expected from the exclusions of birds, bats and monkeys from natural versus human-modified landscapes. Solid arrows represent negative effects, thicker arrows indicate stronger effects, while dashed arrows reduced effects caused by the experiments. (b) Treatment cages at a natural landscape setting. (c) Photos showing the four treatment cages in the human-modified landscape setting

flowering and flowering as well as nut development takes place on racemes, where flowers are born in numbers of 100–300 along an axis (Trueman, 2013). Main insect pests are several Heteroptera species, namely the two-spotted stink bug *Bathycoelia distincta*, the green vegetable bug *Nezara viridula*, the yellow edged stink bug *Chinavia pallidoconspersa* and the coconut bug *Pseudotheraptus wayi*, as well as two Lepidopteran species, the macadamia nut borer *Cryptophlebia batracopha* and the false coddling moth *Thaumatotibia leucotreta* (Schoeman & de Villiers, 2015). Insect damage has not only the direct effect of spoiling the kernel, but also indirect effects of promoting immature nut drop, kernel germination and fungus infestation (La Croix & Thindwa, 1986; Nagao et al., 1992; Schoeman & de Villiers, 2015).

Bats are known to be active in South African macadamia orchards and to feed on major insect pest species, like the green vegetable bug (Taylor, Bohmann, et al., 2013; Taylor et al., 2017). Other data confirm the consumption of several more insect pests by bats (Weier et al., 2019), namely the macadamia nut borer, the two-spotted stink bug and the litchi moth *Cryptophlebia peltastica*. Sixty six percent of the local bat community has been recorded inside macadamia orchards, with 14 identified species classified as either clutter-edge or open-air feeders, while seasonal activity patterns of bats seem to be linked to pest insect abundances (Taylor, Monadjem, & Steyn, 2013; Weier, Grass, Linden, Tscharntke, & Taylor, 2018). Common insectivorous birds in the study region amongst others are the Black-backed Puffback *Dryoscopus cubla*, Cape White-eye *Zosterops capensis*, Tawny-flanked Prinia *Prinia subflava*, Gorgeous Bush-shrike *Telephorus quadricolor*, Red-chested Cuckoo *Cuculus solitarius* or the Brown-hooded Kingfisher *Halcyon albiventris* (Symes & Perrin, 2008; Symes, Venter, & Perrin, 2000), which are presumably also foraging in macadamia orchards. Studies of bird species richness and activity in macadamia orchards in South Africa are lacking, but birds in Australia are known to feed on macadamia pest species like the green vegetable bug (Crisol-Martínez, Moreno-Moyano, Wormington, Brown, & Stanley, 2016). In other agricultural systems, proximity to natural forests was one of the main drivers for bird diversity and predation success (Maas, Tscharntke, Saleh, Dwi Putra, & Clough, 2015). We can hence assume that birds play an important role for biocontrol of macadamia pests and that natural vegetation can influence its extent. Grey-headed parrots *Poicephalus fusciollis suahelicus*, which are frugivorous, have previously been observed in the study area but do not feed on any macadamia flowers or fruits (Symes & Perrin, 2003).

Lying at the foothills of the Soutpansberg mountain range, which has been declared a centre of endemism and biodiversity (Mostert et al., 2008) and part of the Vhembe Biosphere Reserve proclaimed by UNESCO in 2011, Levubu is home to the chacma baboon (*Papio ursinus*), the samango monkey *Cercopithecus albogularis* and the vervet monkey. A survey by the South African Macadamia Growers Association on problem animals showed that monkeys seem to be causing higher damages than baboons (Southern African Macadamia Growers' Association, unpublished data). Communications with farmers confirmed this result and identified vervet monkeys as the most problematic animal to macadamia growers. In this study we therefore focus on the effect of monkeys as crop raiders, particularly vervet monkeys, as samango monkeys are rare and at this stage not considered a pest. Baboons are only encountered on farms on the mountain and were absent from our study sites. Vervet monkeys are reported a crop pest in almost their entire range (Healy & Nijman, 2014). Vervets are widely distributed throughout Africa and can be found in a variety of habitats (Estes & Otte, 2012; Skinner & Chimimba, 2005). Due to their relatively small size they are however dependent on trees and although they do come to the ground, they remain around forest edges for safety (Estes & Otte, 2012; Skinner & Chimimba, 2005). Vervet monkeys are diurnal, usually occur in troop sizes of about 25 individuals and are mostly vegetarian (Estes & Otte, 2012; Skinner & Chimimba, 2005).

The experiments were conducted on six commercial macadamia farms (see Appendix S1 for selection criteria). Macadamia orchards are planted alley-like in rows, with typical spacing of 8m between individual trees and 4m between rows. We compared natural to human-modified landscape settings within each farm (Figure 1). Human-modified landscapes included continuous crops of macadamias or other orchards (e.g. avocado Persea and pecan Carya), some disrupted by roads. Natural landscapes consisted of macadamia trees bordering patches of natural vegetation, which are dense corridors of natural bush, between 98 and 205 m broad and up to 20 ha in extent. The dominant vegetation type in the natural landscape setting comprised 80% (*SD* ±18%) natural bushveld, while at the human-modified landscape natural vegetation comprised only 27 ± 19% or less of the surrounding habitat (Grass et al., 2018). These natural areas still harbour wildlife, including several small antelopes, bushpigs *Potamochoerus larvatus* and vervet monkeys. As monkeys are very vigilant, they stay in the first few rows of the orchard, not moving far away from their natural refuge. Previous studies show that crop raiding of vervets is limited to forest edges with no records at or beyond 200 m forest distance (Saj et al., 2001) or average maximum distances of 15 m with a range of 3–90 m (Wallace & Hill, 2012). Human-modified landscape settings were located at distances between 156 and 527 m away from natural vegetation and were therefore never visited by monkeys.

2.2 | Experimental set-up

The experimental exclusion took place over three consecutive seasons, from September 2015 to May 2018. A total of 48 cages were constructed, each enclosing two macadamia trees with nylon mesh net that would allow for arthropods or small animals but excluded flying vertebrates, monkeys and large herbivores (see Appendix S1). We applied four treatments. The "Full" exclosure was closed at all times, thereby preventing all bats, birds and monkeys from accessing the trees. The "Day" and "Night" exclosures were only closed either during the day or night excluding either diurnal birds and monkeys or bats and nocturnal birds (namely nightjars, Caprimulgidae or small owls, Strigidae and Tytonidae) respectively. Additionally, "Control" cages were open at all times, consisting of a frame without nets. On each farm a set of four exclosures (Full, Day, Night, Open Control) was put up at a human-modified landscape setting and one at the natural landscape (Figure 1b,c). The design resulted in 12 sets of four treatment exclosures, hence 48 cages excluding a total of 96 macadamia trees. In the third year of this study the sets were reduced to only full and control treatments, resulting in a reduced number of treatment cages of 20 over five farms in the final year (see Appendix S1).

2.3 | Yield

Macadamia nuts drop continuously over several months once matured and are then harvested off the ground (Nagao et al., 1992). To isolate the effect of vervet monkeys, which feed on immature nuts off the tree, from that of other animals, which feed on fallen nuts, we applied an indirect yield measure by counting and monitoring nut sets on the trees. In the season of 2016/2017 we marked 50 racemes on each tree early in the season, counted all nuts per raceme and monitored the number per racemes until the nuts had completely matured. This resulted in a final average nuts/50 raceme count prior to harvest. Nut set (final number of nuts per raceme) was analysed using generalized linear mixed models (GLMM, binomial error structure), with treatment and landscape as fixed factor and farm as random factor (Table S1). Each landscape setting was then analysed separately to allow for multiple comparisons of means by treatment using Tukey contrasts (Table 2). The final nut set was extrapolated to yield in kg per hectare (see Appendix S3).

2.4 | Nut quality

Macadamia nuts were collected from within each experimental cage over the three consecutive seasons (2016–2018). Samples (mean ± *SD*: 1,672.33 ± 497.28 g) were taken per experimental cage, cracked and the kernel checked for any quality defects. Total sample

TABLE 1 Summary of results obtained from each landscape setting and treatment combination. Experimental outcome for mean nut set, estimated yield (as a function of nut set), % unsound kernel (UKR) and income/h/year (as a function of both yield and UKR)

Landscape	Treatment	Nut set (total/50 racemes)	Yield (kg/ha)	UKR (%)	Income (USD/ha)
Human-modified	Full	43.93	862.76	6.9	3,154.42
	Night	77.88	1,529.52	6.45	5,719.96
	Day	59.26	1,163.83	7.13	4,204.78
	Control	107.06	2,102.60	5.74	8,141.57
Natural	Full	35.27	1,303.97	6.28	4,917.84
	Night	6.67	246.60	5.36	972.34
	Day	62.94	2,326.96	6.29	8,771.63
	Control	46.33	1,712.87	4.04	7,175.66

weight as well as shell and kernel weight were recorded. Total kernel weight was divided into sound (not damaged) and unsound (defected) kernel. The quality (mass unsound kernel to total sample mass) data were analysed using generalized linear mixed modelling (GLMM, binomial error structure) with treatment and landscape setting as fixed factors and farm as random factor (Table S1). Each landscape setting was then analysed separately to allow for multiple comparisons of means by treatment using Tukey contrasts (Table 2). The inverse logit values of the binomial model outcomes are interpreted as "unsound kernel", a common measure of quality in the industry, which refers to the percentage unsound kernel within the total in-shell sample. All statistical analyses were performed in R (v. 3.5, R Foundation for Statistical Computing, Vienna, Austria) using packages "lme4" version 1.1–14 (Bates, Maechler, Bolker, & Walker, 2015) and "multcomp" version 1.4–7 (Hothorn, Bretz, & Westfall, 2008).

2.5 | Economic impact

Income per hectare was calculated by using the mean yield and percentage unsound kernel per landscape and treatment combination. Quality determined the price per kg, which was then multiplied by the yield per hectare (see Appendix S4 – Income calculation).

3 | RESULTS

Since monkeys were absent from the human-modified landscape settings, the observed treatment effects were solely due to the exclusion of bats and birds, while effects at the natural setting included the impacts of crop raids by monkeys. Monkeys furthermore only affected the yield, but not the quality of nuts.

3.1 | Yield

Final nut set was generally lower in the natural landscape setting than in the human-modified landscape ($p < 0.001$) and significantly influenced by the interaction ($p < 0.001$) of treatment and landscape (Table S1). Yield was 19% lower in the natural control than in the human-modified control (based on values in Table 1). In the human-modified landscape setting, full and day treatments resulted in a significantly lower nut set relative to the control ($p < 0.001$; Table 2 and Figure 2a), while the night treatment did not significantly differ ($p = 0.39$) from the control. The full exclosure, where bats and birds were both excluded, resulted in the lowest nut set, followed by Day and then Night. The exclusion of both bats and birds resulted in a 60% decrease in yield compared to the control (Table 1).

TABLE 2 Tukey post hoc test results of nut set and quality effects separate for landscape settings

Landscape	Treatment	Estimate	*SE*	*z*-value	*p*-value
Nut set: Fit: glmer (formula = Nuts/raceme ~ Treatment + (1|Farm), family = "binomial")					
Human-modified	Day–Control	−0.47	0.65	−7.24	<0.001
	Full–Control	−0.69	0.07	−9.78	<0.001
	Night–Control	−0.17	0.06	−2.66	0.39
	Full–Day	−0.23	0.07	−3.13	0.0095
	Night–Day	0.30	0.66	4.50	<0.001
	Night–Full	0.52	0.71	7.32	<0.001
Natural	Day–Control	0.32	0.07	4.35	<1e−04
	Full–Control	−0.08	0.08	−0.94	0.77
	Night–Control	−0.83	0.17	−5.03	<1e−04
	Full–Day	−0.40	0.08	−4.98	<1e−04
	Night–Day	−1.15	0.16	−7.18	<1e−04
	Night–Full	−0.76	0.17	−4.55	<1e−04
Nut quality: Fit: glmer (formula = Unsound/total ~ Treatment + (1|Farm), family = "binomial")					
Human-modified	Day–Control	0.23	0.04	6.60	<0.001
	Full–Control	0.20	0.03	5.94	<0.001
	Night–Control	0.12	0.04	3.44	0.0023
	Full–Day	−0.04	0.03	−1.06	0.291
	Night–Day	−0.11	0.04	−2.10	0.0082
	Night–Full	−0.07	0.03	−2.14	0.0651
Natural	Day–Control	0.47	0.04	10.74	<0.001
	Full–Control	0.46	0.05	9.66	<0.001
	Night–Control	0.30	0.05	6.04	<0.001
	Full–Day	−0.001	0.05	−0.03	0.98
	Night–Day	−0.17	0.05	−3.62	0.0009
	Night–Full	−0.17	0.05	−3.20	0.003

In the natural landscape setting, where monkeys were present, the full exclosure did not significantly differ from the control ($p = 0.77$; Table 2 and Figure 2b). In the day exclosure on the other hand, we did observe a yield increase (26%) and nut set was significantly higher ($p < 0.001$) than in the control (Table 2 and Figure 2b). Here monkeys were excluded, while simultaneously allowing for some pest control by nocturnal birds and bats. The night exclosure, where only nocturnal vertebrates were excluded, showed a significantly lower ($p < 0.001$) nut set relative to the control (Table 2 and Figure 2b).

3.2 | Nut quality

Quality of nuts was generally better in the natural setting, compared to the human-modified landscape ($p < 0.001$), with 4.04% unsound kernel compared to 5.74% in the two controls (Table 1 and Table S1; Figure 2c,d). In both landscape settings all exclusions resulted in significant increases in unsound kernel (all $p \leq 0.002$; Tables 1 and 2). The combined effect of the full exclusion resulted in the lowest quality (highest percent of unsound kernel), followed by the day and then night treatment (Table S1; Figure 2c,d). Treatment effects were stronger in the natural landscape setting with higher differences in defect kernel between treatments (Table 1).

3.3 | Economic impact

All income values are expressed as kg/ha/year (Table 1) and combine both yield and quality effects (Figure 3). Income impacts generally followed the observed differences in yield. In the human-modified landscape setting the exclusion of both bats and birds resulted in an income loss of USD 4,987.15/ha and reduced income losses for the exclusion of either diurnal birds (USD 3,936.80/ha) or bats and nocturnal birds (USD 2,421.61/ha). In the natural landscape setting the full exclosure resulted in an income loss of USD 2,257.83/ha. While the yield differences between full and control were not significant, it still showed a negative trend where all vertebrates were excluded. The day exclosure resulted in an income gain of USD 1,595.96/ha.

4 | DISCUSSION

Our study shows that the profits of biocontrol outweigh the losses from crop raiding monkeys, while both are promoted by natural vegetation. The exclusion of bats and birds led to a decrease in yield as well as quality in both landscape settings, while the exclusion of monkeys only resulted in yield gains close to natural vegetation. In

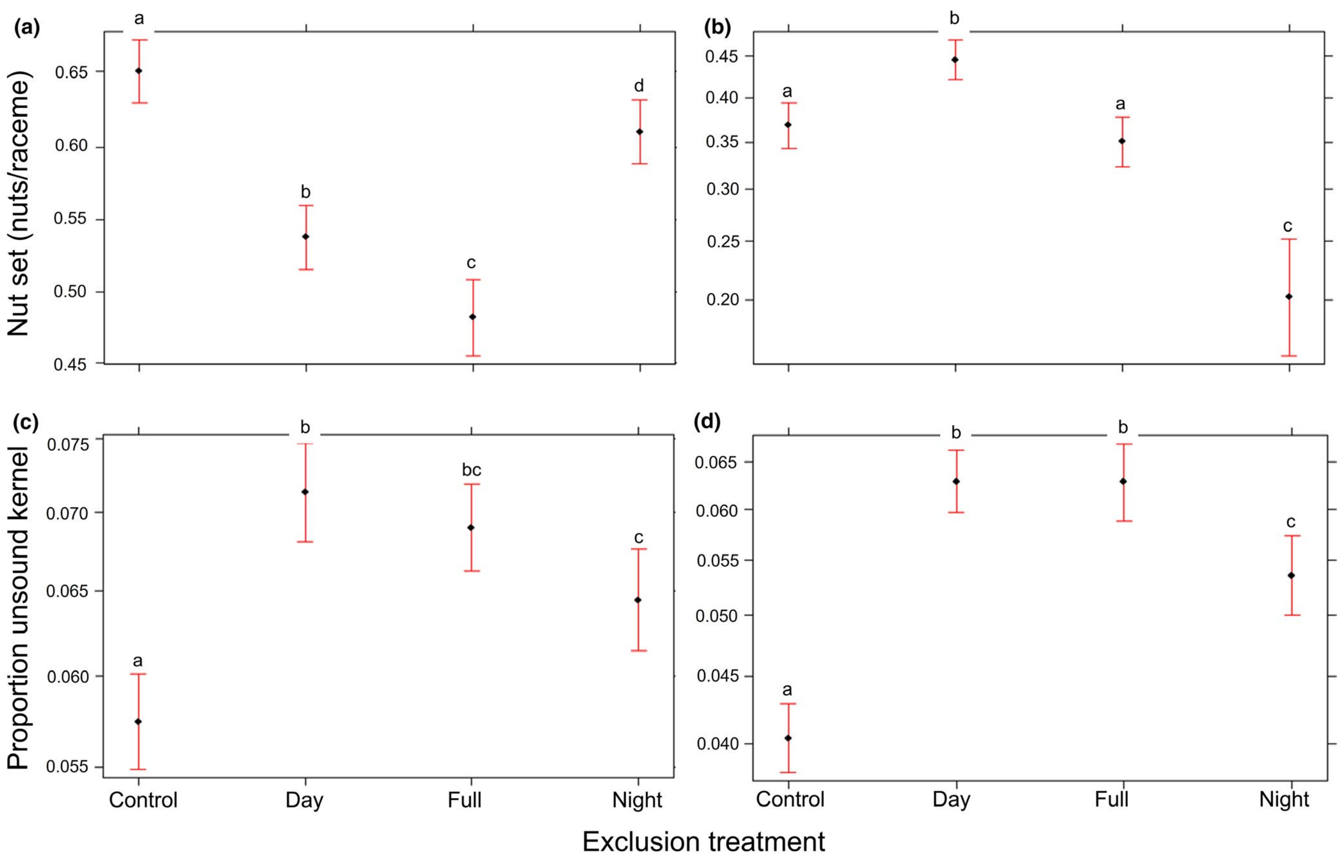
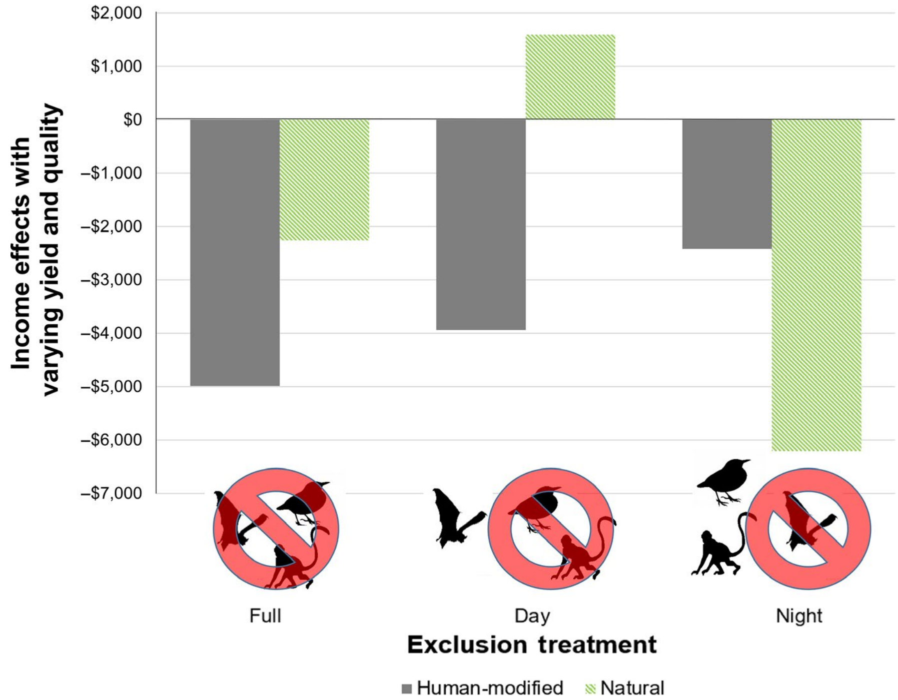


FIGURE 2 Model results for nut set (a & b) and quality (c & d) per landscape setting and treatment with SE. (a) Nut set at human-modified setting, (b) nut set at natural setting, (c) proportion unsound kernel in human-modified setting, (d) proportion unsound kernel in natural setting. Annotated letters show significant differences between treatment groups (different letters) and same letters for no significant treatment differences

FIGURE 3 Income effects (losses and gains) resulting from varying yield and quality over treatment and landscape setting, respective to each control



the human-modified setting the exclusion of bats and birds resulted in yield drops of 60% or losses of about USD 5,000/ha. The exclusion of monkeys in natural settings on the other hand led to an increased yield of 26% and income of about USD 1,600/ha.

The results of nut quality generally confirmed our expectation of stronger biological control by bats and birds near natural vegetation. We found lower proportions of unsound kernel (−1.7%) in natural landscape settings compared to the human-modified one and reduced qualities for all treatments in both landscape settings. Nut quality values were generally realistic and comparable to the average of 4.5% defect kernel for 2017 in the study area, as given by the local processing facility (Green Farms Nut Company, personal communication, 4 September 2018). The observed effects clearly show the importance of natural areas to the efficiency and effectiveness of biocontrol agents. The importance of these landscape features and connectivity within an agricultural landscape for bats has been highlighted in previous studies (Frey-Ehrenbold, Bontadina, Arlettaz, & Obrist, 2013; Kelly, Kitzes, Wilson, & Merenlender, 2016; Wordley, Sankaran, Mudappa, & Altringham, 2017).

Yield effects at the human-modified landscape settings follow a clear pattern and match our predictions that yield would decrease significantly where bats and/or birds were excluded. The combined exclusion of bats and birds, however, resulted in the largest effect and a yield drop of about 1,240 kg/ha (60%) compared to the control. Diurnal birds furthermore seemed to play a larger role for biological control than bats and nocturnal birds, as quality as well as yield effects were larger in the day exclosure.

In the natural landscape setting effects by monkeys greatly changed the pattern of yield differences. Pest control services by bats and birds seemed to outweigh crop raiding effects by monkeys and the exclusion of both, although not significant, still resulted in yield decreases, due to lacking biocontrol. The exclusion of monkeys in the day exclosure resulted in yield increases of 614 kg/ha (26%). Although partially weakened by the simultaneous exclusion of diurnal birds, this effect was far less than the great impact bats and birds had in the human-modified landscape.

Our observations are in line with other studies (Naughton-Treves et al., 1998; Saj et al., 2001; Tweheyo et al., 2005), which show that crop raiding by monkeys is limited to the vicinity of forest edges. This was also true in macadamia orchards as no positive yield effects could be observed in any exclusion experiments at the human-modified landscape. Vervet monkeys and other primate species are, however, not only considered a pest to macadamias but also to many other crops in Africa (Ango et al., 2017; McGuinness & Taylor, 2014; Wallace & Hill, 2012). While their preferences for various crops might differ and, thereby, the extent of the caused damages, our results give a general indication for other crops on the possible threat by monkeys and the simultaneous compensation by beneficial insect pest control, both stemming from natural areas.

Since yield had a stronger impact on income calculations than had quality, profit differences roughly follow the pattern we observed in yield. Income is generally lower in natural landscape settings compared to human-modified landscapes, due to extreme yield drops caused by monkeys. Prevented biological control of both bats and birds combined resulted in an income loss of about USD 5,000/ha at the human-modified setting, whereas prevented monkey damage at the natural setting amounts to an estimated USD 1,600/ha income gain. The exclusion of vertebrates near natural vegetation can hence enhance yield, but the loss of an ES like biological control would have a higher economic impact than the prevention of an EDS like crop raiding by monkeys. Taylor et al. (2018) estimates the value of bats in the South African macadamia industry through an avoided cost model to be up to USD 139/ha for direct avoided costs. This is considerably lower than our estimations, even when just considering the effects of the night exclosure at human-modified settings of USD 2,422/ha. This may be due to the contribution of nocturnal insectivorous birds which was not considered by Taylor et al. (2018) and the fact that birds generally seem to have a higher effect than bats. Likewise this model only considered bat predation effects on one pest, while our exclusion experiments captured the effect of all pest insect species on quality and yield. This highlights the importance of experimental research as guideline and confirmation of theoretical models.

In our study we assess a trade-off relationship between specific ES and EDS of two independent functional groups. While previous work (Saunders & Luck, 2016; Saunders et al., 2016) already show that ES can vary over season and with functional group and that ES can be compromised by EDS, we highlight the contrasting impact of unrelated taxonomic groups, birds, bats and monkeys. All three are enhanced by natural vegetation. Where farmers are encouraged to support ES, there is potential for disadvantages through EDS. The extent to which ES outweighed EDS in this scenario gives hope and confidence that this will not compromise conservation efforts. It should therefore be the aim of future research to consider the interactions of ES and EDS of all participating functional groups as a whole, to be able to assess the real impact of biodiversity to agricultural or other systems.

Overall it is advisable to maintain and possibly increase the amount of natural vegetation around agricultural areas, considering the significantly higher pest control services. Crop raiding damages can, however, be much more visible and more perceived by affected farmers, causing many farmers to view natural areas as loss or cost (Tscharntke et al., 2016). Studies looking into possible mitigation strategies are therefore highly advised, to avoid negative associations with natural areas.

One suggested mitigation strategy is the establishment of buffer zones between natural areas and palatable crops to prevent crop raiding (Naughton-Treves et al., 1998; Saj et al., 2001). By doing so, one compromises the beneficial ES stemming from natural landscapes and in this case the highly profitable service of biological control by bats and birds. Connectivity between natural areas and the orchards should therefore be maintained. Other ES, like pollination, could also be enhanced by natural vegetation and be compromised by its removal or isolation. Primate proof fences are another alternative, which simultaneously exclude other herbivores and pest species. These are, however, associated with high costs and thereby only available to some commercial, large-scale farmers. Guarding of crops is a very popular mitigation strategy (Ango et al., 2017; Warren, Buba, & Ross, 2007), which can, similar to the exposure of scare crows, also affect birds and their willingness to feed in the orchards. Education is therefore one of the most important tools in protecting natural areas around agricultural land and the information of landowners about its valuable benefits, which can be more plentiful than its costs. To further promote bird and bat populations and thereby potentially increase the value of biological control, artificial nesting and roosting sites can be provided to encourage them to inhabit agricultural areas, where natural habitat is scarce (Mols & Visser, 2007). This can be more cost efficient than pesticide treatments in keeping pest species under a certain threshold (Puig-Montserrat et al., 2015). Research towards species richness in specific agricultural areas is needed to be able to provide appropriate designs.

5 | CONCLUSIONS

Our study showed the great impact of bats and birds as biocontrol agents in agricultural systems, which can be compromised, but not outweighed, by monkeys when natural vegetation is close. While ecosystem disservices by monkeys are limited to only the close proximity of natural vegetation, ES by bats and birds, originating also from these natural areas, still have substantial economic impacts in human-modified landscapes and actually outweigh negative impacts by monkeys. Remaining patches of natural vegetation, harbouring both ES and EDS, can therefore still be viewed as highly beneficial to agriculture. Since crop raiding effects are more visible, it is still of high importance to research effective monkey mitigation strategies that can then be made available to farmers. Our findings are applicable to many agricultural systems, where monkey and primate species are considered a pest. Areas like the tropics and subtropical regions, where primate species are distributed are also areas with high general, but also bird and bat species richness and diversity. We can therefore assume similar counterbalancing effects between biological control and crop damages by monkeys, to what we have observed in macadamia orchards.

It is important to make growers aware of threats as well as economic benefits natural areas pose for them. By protecting surrounding natural bush and erecting low budget artificial roost and nest sites, these farmers can play an important role in species conservation, as it is a serious and affordable alternative to significantly increase your profits as a farmer.

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AUTHORS' CONTRIBUTIONS

V.M.G.L. planned and executed the experiments, performed data analysis and wrote the first draft of the manuscript. E.J. provided yield projections. I.G. and T.T. took part in the planning and set up of the project and I.G. assisted in the statistical analysis. S.M.W. participated in the set-up of the project and data collection. P.J.T. acted as project supervisor. All authors contributed critically to the writing of this manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository. https://doi.org/10.5061/dryad.m225sc0 (Linden et al., 2019).

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